American Fern Journal

Vol. 18 JULY–SEPTEMBER, 1928 No. 3

Fluctuation in Equisetum*

John H. Schaffner

In making a comprehensive study of the taxonomy of plants, the fact becomes evident that there is no general correspondence between the taxonomic system and the phylogenetic process, or evolution, on the one hand, and the environment or utility, on the other. The evolutionary movement, in the broad sense, goes on in the same direction in widely diverse environments. The same progressive movements also take place independently of special morphological differences and often at different evolutionary horizons, as, for example, the origin of the flower or determinate reproductive axis. But another fact stands out with equal prominence. There is abundant ecological adaptation, as ability to withstand drought or cold, and also great fluctuation or ecological variation of the individual in many groups. In some the ontogeny is often remarkably influenced by the environment. Of all the groups of plants, which the writer has studied, the *Equisetaceae* seem to possess the greatest ability to fluctuate; and it is very important that those who are doing morphological or taxonomic work on the group take adequate account of this tendency to fluctua-

* Papers from the Department of Botany, The Ohio State University, No. 217. [Volume 18, No. 2, of the Journal, pages 37–68, plate 1, was issued July 12, 1928.]

tion. It is often very great in characters that we are accustomed to think of as quite constant. This is probably due to the fact that *Equisetum* represents a primitive group which has developed a large number of specializations and even of advanced characters.

The keynote to the situation is primitive position in respect to fundamental evolutionary progression combined with important specializations. Among these specializations may be mentioned: development of prominent internodes and internodal cavities; development of leaf sheaths with loss of proper leaves; development of sterile and fertile shoots; development of branch whorls, and their suppression, on top of the more primitive sporadic monopodial branching system; the evolution of a peduncle and primitive perianth; and specialization in the loss of chlorophyll in the cone, peduncle, and reproductive shoot. *Equisetum* can, therefore, be defined as a specialized, primitive vascular plant.

If one studies the progressive changes in the various plant phyla, one soon finds that the first steps in a given direction are commonly much more subject to fluctuation than the more advanced evolutionary stages of the same category. Thus a primitive flower, like the cone of a Lycopod, Equisetum, Araucarian, or Larix, or even of a Rose, will frequently proliferate, returning to the primitive indeterminate condition, while such a development is exceedingly rare and practically impossible in the higher types of strobili and advanced flowers. The same condition holds in the dimorphism between foliage leaf and sporophyll. Intermediate expressions between leaf and sporophyll are rather common in such low forms as *Osmunda cinnamomea* and *Onoclea sensibilis,* while such intermediate forms would be very difficult to find in any advanced group unless a mutative change occurs. A primitive flower, which is just one step removed from the original indeterminate condition, has great variability in the number of its sporophylls while a high type of flower has its parts exceedingly constant.

Since *Equisetum* has such a large number of these first steps in evolutionary advancement, one would expect the genus to be ideal for the study of fluctuation, and according to the writer's observation, as intimated above, its species appears to have a greater supply of important fluctuations than almost any other vascular plants. The real difficulty in studying *Equisetum* is to find something that can be depended upon.

1. FLUCTUATION IN THE SHEATH SEGMENTS AND INTERNODAL RIDGES. In most of the species the variability in these characters is very great, the numbers depending largely on the comparative size of the growing bud. It is only when the extreme species of the several phyletic series are reached that something like the stability characteristic of corresponding structures of higher plants is attained. In *E. praealtum* the teeth and ridges vary from 7 to 48, or even beyond these limits; in *E. variegatum* the numbers usually fluctuate between 5 to 12; while in E. *scirpoides*, the culmination of this species group, there are 6 ridges (3 double ridges) and 3 sheath segments and teeth quite regularly. In the more highly evolved EQUISETA HETEROPHYADICA, although the main stem is still quite variable, the normal branches approach a condition of constancy in sheath segments and internodal ridges, *E. pratense* mostly having 3 and *E. arvense* 3 or 4.

2. DISCOLORATION OF SHEATHS. No reliance is to be placed on the color patterns of the sheaths or sheath teeth of such species as *E. laevigatum, E. praealtum, E. hiemale* and *E. kansanum,* although these are frequently emphasized in keys and descriptions. In *E. praealtum* the whole sheath may be black or dark brown, or it may

be black with a very narrow white band at the base; it may be uniformly white or ash-colored; it may be light colored with a dark band above or below or with a band at both ends. *E. hiemale* shows similar fluctuations. Often several of these patterns will be on the same shoot. *E. laevigatum* typically has green sheaths until quite old, with narrow brown spots on the tips of the leaf segments, but the basal sheaths are often discolored in the same patterns developed in *E. praealtum*.

3. ABSCISSION OF SHEATH-TEETH. In those species which have deciduous teeth the formation of abscission layers is very variable both as to time of formation and completeness of the development. The condition ranges all the way from caducous to persistent teeth. In *E. praealtum* and *E. laevigatum* the abscission frequently occurs very early and the adnate teeth are carried up on the tip of the stem as "pagoda caps"; but often the teeth are long persistent and are still present as distinct appendages on old sheaths. In other cases, although the stem grows through the whorl of teeth, they soon drop off as individual members. Frequently the lowest sheaths have persistent teeth without any abscission layer developing.

4. FLUCTUATION IN LENGTH OF INTERNODES. The difference in length of internodes in a species is very great, and the fluctuation on a single shoot is often enormous, ranging from practically zero length to 5¼ inches and more in *E. praealtum*. In *E. praealtum*, *E. hiemale*, and *E. laevigatum* there may be two, three, four or more sheaths completely telescoped through lack of internodal development. Sometimes a zone of short internodes appears suddenly and ends suddenly, or the zone may show a gradual succession of elongating or shortening internodes. These zones may be near the base of the shoot, in the middle, or near the tip; or there may be

two or more such zones. Occasionally one can find a patch of plants in which nearly all of the shoots of a given year have a contracted zone in about the same region of the shoot, indicating some strong environmental influence acting at the time of development. Plants are also often developed quite regularly. In patches of *E. praealtum* with prevailingly white sheaths, the bands of shortened internodes present a striking appearance.

These short internodes are commonly discolored on the inner wall of the central cavity. Sometimes the color is yellowish-brown and sometimes very dark brown or nearly black. Occasionally, however, one or more cavities or even all in a zone may have the normal white appearance of the normal central cavity. The walls of the short cavity are also sometimes granular. This suggested that the short internodes might be caused by some sort of insect. But no evidence of any kind has been found.

5. FLUCTUATION IN BRANCH WHORLS. Those species which have regular whorls of branches often show striking variation in this character. This is especially true for *E. fluviatile* and *E. palustre,* either of which may show extensive branching with regular whorls, may be sporadically branched or may show no branching of the aerial shoot at all. The number of whorls of branches and their nearness to the base or apex is also exceedingly variable. There is also much fluctuation in the development of secondary branches. Compound branches are very common in *E. arvense* and of many degrees of complexity, while *E. silvaticum,* which normally has compound branches, may be simply branched. The whorled branch condition, phylogenetically considered, is an advanced condition imposed on a system with sporadic branching, as manifested in the rhizome.

6. GENERAL HABIT. The general habit varies greatly in most species, and especially in *E. fluviatile, E. palustre, E. laevigatum, E. kansanum, E. silvaticum, E. pratense, E. telmateia,* and *E. arvense.* In *E. silvaticum, E. pratense,* and *E. arvense,* the shoots may be tall with regular whorls of long or short branches; they may be irregularly branched and bushy or closely tufted, or they may even develop as typical mat plants lying flat on the ground with the main branches radiating from the center.

7. FLUCTUATION IN THE SILEX. The development of the silicious crust is very variable also, some individuals being comparatively smooth while others are exceedingly rough. There is often a considerable regional difference in this respect.

8. AMPLIATED SHEATH. In general the sheaths may be described as ampliated or tight. But the close-fitting, cylindrical sheaths are usually also ampliated or funnel-shaped when young, and may thus cause difficulty in determination. Well-developed specimens alone can give definite information as to the real nature of the sheath in a number of species.

9. INTERGRADATION BETWEEN VEGETATIVE AND FLORAL SHOOTS. All Equiseta have a dimorphism of shoots, definite, determinate, vegetative shoots and determinate reproductive or cone-bearing shoots. Since there is a rather primitive type of cone development, one would naturally expect to find some fluctuation between the two conditions. One is, however, hardly prepared for the extreme series of ontogenetic expressions, present in many species, by which every gradation of size and perfection is produced between the normal fertile cones and the determinate, vegetative tip. The sterile and semi-sterile cones vary from the size of a pin head to the size normal for the fertile cones of the species. The smallest

cones are on shoots with very slender tips. These fluctuating series are common in *E. laevigatum, E. praealtum, E. kansanum, E. fluviatile, E. palustre,* and even *E. pratense.* There are also integrading cone series in *E. silvaticum* and *E. arvense,* but they are rather rare in comparison with their frequency in such more primitive species as *E. praealtum, E. fluviatile,* and *E. palustre.*

These semi-sterile cones have in the past given rise to much speculation as to possible hybrid races in *Equisetum.* The forms known as *E. trachiodon, E. litorale,* and *E. variegatum jesupi* have been regarded as hybrids, apparently mainly because of imperfect spores and sporangia. There may be hybrids in *Equisetum* but, so far, I myself have never found any definite evidence of it. The way to settle the question is for someone to attempt the hybridizations. In attempting to discover possible hybrids, systematists must also learn to judge of the supposed hybrid characters by the modern principles of genetics and Mendelian heredity. The mere presence of semi-sterile shoots and of intermediate characters does not constitute evidence of hybridity in *Equisetum.*

10. THE CALYX AND SPOROPHYLLS. The *Equisetum* cone is made up of a series of separate sporophylls arranged in spirals and so placed that they fall into definite cycles. The numbers in a whorl usually decrease slightly from the middle to the base and decidedly so to the tip. A cone may have as few as 10 free sporophylls (minute sterile type) or even less, or as many as 214 or more in the large normal cones of *E. praealtum.* At the base there is a special sheath or calyx of united sporophylls bearing sporangia only on the upper side. The enormous fluctuation in the determinate growth of the cone is probably due to the fact that *Equisetum* has not evolved very far from the primitive indeterminate type.

The acquired potentiality of determination does not work promptly or accurately. Hence there is also much proliferation in some species, as in *E. fluviatile.* In the lower species, the calyx segments are normally all sporangium-bearing. Nevertheless in species like *E. praealtum* part of the segments may be completely sterile, and in extreme cases, although rarely, a completely sterile calyx is developed. This development of a special whorl of leaves between the sporophylls and vegetative leaves is one of the characteristics of the higher flowers.

In the highest Equiseta the calyx is normally entirely sterile and it is only occasionally that one can find one or more sporangia on it. In *E. arvense* and *E. pratense* one side of the bud may be more advanced than the other, so the sheath below the cone may be leaf sheath on one side and sterile calyx on the other. In such cases then the segments of the calyx in line above will also show the more advanced gradient and will have sporangia on the upper side, while the segments in line with the normal leaf sheath segments below will be sterile.

11. THE PEDUNCLE. The lower Equiseta usually have the cone sessile or nearly so in the uppermost leaf sheath, as can be observed in *E. laevigatum, E. praealtum,* and *E. hiemale.* The internode between the last leaf sheath and the calyx is commonly not more than one-fourth inch long. But beginning with the species with annual aerial shoots a peduncle is evolved which reaches its maximum in *E. telmateia* and *E. arvense.* In *E. kansanum,* and *E. fluviatile* the peduncle is often distinct and of some length, while in *E. palustre, E. silvaticum,* and *E. pratense* it is usually prominent. In all cases the fluctuation in length is very great. In the lower species the peduncle also fluctuates in texture and color from the ordinary green to yellowish and brown. In *E. arvense* the fluctuation in length is from less than one-half inch up to five inches and more.

12. TERMINAL POINT OF CONE. The lower Equiseta have apiculate cones while the higher species have rounded tips or are merely acute. Since *E. kansanum* and *E. funstoni* have apparently originated from the apiculate group and have eliminated the point with the acquisition of annual aerial shoots, this character becomes of diagnostic value, but, alas, just as is the case with the newly acquired sterile calyx and peduncle, so also can no absolute reliance be placed on the presence or absence of the apiculate cone, as in distinguishing between *E. laevigatum* and *E. kansanum*. For although the difference in this character is usually definite, extreme fluctuations overlap and one must, therefore, depend in such cases on the annual and perennial conditions of the stems. The development of the projection at the apex of the cone is to be understood as due to a slow process of determination. In the higher Equiseta determination of the floral axis is more prompt and definite and the point is thus eliminated, because the universal trend of floral evolution in all groups is to a more prompt cessation of growth after reproduction begins, until in the highest, epigynous type the central point of the floral axis actually stops growing before the incepts of the floral leaves have made their appearance.

13. LOSS OF CHLOROPHYLL IN REPRODUCTIVE SHOOT. In the lower species of *Equisetum* the cone is green until the spores reach maturity. As one ascends the scale, the loss of green color is shoved back farther and farther in the ontogeny until the extreme is reached in *E. telmateia* and *E. arvense,* where the entire reproductive shoot is normally without chlorophyll or with only very slight chlorophyll development. Along with the loss of chlorophyll goes the loss of the branch whorls in these species. But fluctuation is again prominent, for one can frequently find fertile shoots with varying degrees of branch development and varying degrees of chlorophyll.

Now, considering all this mass of fluctuating characters, where is one to turn to find something dependable for species characterization and delimitation? There are such characters which show no greater fluctuation than is present commonly in more fixed groups. These characters must be found and emphasized in keys and descriptions. And when this is done there is little left for varieties. There are practically no varieties in *Equisetum*. Yet a great number of them have been described. Seventy years ago Milde found 11 in *E. arvense*, 9 in *E. telmateia*, 34 in *E. ramosissimum*, 12 in *E. hiemale*, 13 in *E. variegatum*, 7 in *E. palustre* and 3 in *E. praealtum* (*robustum*). Many more have been described in the mean time. A. A. Eaton, who was our last prominent student of the group, realized that there were practically no good varieties recognizable in *Equisetum*, yet he immediately began to establish a large number of new ones.

Without going into the question of the validity of the taxonomic groups designated as "varieties" and "forms," which have played such a prominent part in the taxonomy of *Equisetum*, it becomes necessary to dispose of the fact of fluctuation in one way or another, whenever one is employed in naming or describing the various species which one may recognize as valid.

The writer is opposed to giving formal names to fluctuations, for it can easily be seen that not only will two shoots from the same rhizome often be placed in different groups but the same shoot must often be catalogued under several varietal names as is at present actually done! Such a procedure seems extremely foolish and the wonder is that it can actually be carried on in the name of taxonomic science.

The writer believes that the situation can be properly met by the use of descriptive polynomials. If Latin descriptive terms are deemed necessary, then the main types of fluctuations can receive general descriptive designations, as *ramulosum, pauciramulosum, multiramulosum, nudum,* etc., to designate the degree of branching; *proliferum* for a proliferated cone; *polystachyum* for the presence of cones on lateral branches; *dichotomum* for a case of branch dichotomy or twinning, etc. Then if one finds an individual of *E. fluviatile* which has a shoot with many whorls of branches, a proliferated cone, and one or more side branches with cones, it would be *E. fluviatile* L. fl. *multiramulosum proliferum polystachyum.* Another shoot from the same rhizome may have no branches whatever but may have a dichotomous tip, each of the twin branches ending in a semi-sterile cone. This would be *E. fluviatile* L. fl. *nudum dichotomum semi-sterile.* In almost any large patch of *E. praealtum* one can find individual shoots with no branches and with a single terminal cone, but commonly or even quite generally, in Ohio, the older shoots develop lateral branches ending in small cones. The first shoot would then be *E. praealtum* Raf. fl. *nudum,* if one would not look for other fluctuating peculiarities, which would, of course, lengthen the designation, and the other type would be *E. praealtum* Raf. fl. *polystachyum.* And so on *ad infinitum.* This is exactly the same kind of taxonomic exercise as when one goes into an apple orchard and makes the unusual discovery that of three trees, one has an abundance of apples, the second one only a single apple, and the third tree no apples at all. This is an exercise in organographic ecology and not taxonomy. From the standpoint of ecology this is a legitimate and important pastime; from the standpoint of formal taxonomy, it is "nonsense botany." For if taxonomy is not naming and establishing larger and smaller groups which reproduce themselves after their kind, then it has no legitimate basis as a science.

Columbus, Ohio